

LETTERS

New Oligocene primate from Saudi Arabia and the divergence of apes and Old World monkeys

Iyad S. Zalmout^{1,2}, William J. Sanders^{1,3}, Laura M. MacLatchy^{1,3}, Gregg F. Gunnell¹, Yahya A. Al-Mufarreh⁴, Mohammad A. Ali⁴, Abdul-Azziz H. Nasser⁴, Abdu M. Al-Masari⁴, Salih A. Al-Sobhi⁴, Ayman O. Nadhra⁴, Adel H. Matari⁴, Jeffrey A. Wilson^{1,2} & Philip D. Gingerich^{1,2,3}

It is widely understood that Hominoidea (apes and humans) and Cercopithecoidea (Old World monkeys) have a common ancestry as Catarrhini deeply rooted in Afro-Arabia^{1–4}. The oldest stem Catarrhini in the fossil record are Propliopithecoidea, known from the late Eocene to early Oligocene epochs (roughly 35–30 Myr ago) of Egypt, Oman and possibly Angola^{5–10}. Genome-based estimates for divergence of hominoids and cercopithecoids range into the early Oligocene¹¹; however, the mid-to-late Oligocene interval from 30 to 23 Myr ago has yielded little fossil evidence documenting the morphology of the last common ancestor of hominoids and cercopithecoids, the timing of their divergence, or the relationship of early stem and crown catarrhines. Here we describe the partial cranium of a new medium-sized (about 15–20 kg) fossil catarrhine, *Saadanius hijazensis*, dated to 29–28 Myr ago. Comparative anatomy and cladistic analysis shows that *Saadanius* is an advanced stem catarrhine close to the base of the hominoid–cercopithecoid clade. *Saadanius* is important for assessing competing hypotheses about the ancestral morphotype for crown catarrhines^{1,12–14}, early catarrhine phylogeny^{12,15} and the age of hominoid–cercopithecoid divergence¹¹. *Saadanius* has a tubular ectotympanic but lacks synapomorphies of either group of crown Catarrhini, and we infer that the hominoid–cercopithecoid split happened later, between 29–28 and 24 Myr ago.

The catarrhine fossil record subsequent to propliopithecoids was unknown except for isolated dentitions of the late-Oligocene *Kamoyapithecus hamiltoni* from Kenya¹⁶ until the Afro-Arabian early Miocene (about 23–16 Myr ago) diversification of apes^{5,16} (considered as basal or ‘eo’¹⁷-hominoids, and/or late stem catarrhines and placed in ‘Proconsuloidea’^{3,12} and ‘Dendropithecoidea’^{3,18}) and cercopithecoids^{2,4} (Supplementary Information). The paucity of fossil evidence from about 30–23 Myr ago has inhibited the testing of competing hypotheses about the attributes of the ancestral morphotype of cercopithecoids and hominoids^{1,12–14}, the age of their divergence¹¹ and the nature of the propliopithecoid–crown-catarrhine relationship^{12,15}.

A new Oligocene catarrhine fossil (SGS-UM 2009-002), preserving substantial facial, palatal and dental morphology, was recently recovered from the top of an oolitic ironstone bone bed of the middle unit of the Shumaysi Formation, at Harrat Al Ujayfa in Al Hijaz Province, western Saudi Arabia (Fig. 1a–c) by a Saudi Geological Survey–University of Michigan expedition. This is the most substantive evidence of catarrhines from the late early Oligocene through to the late Oligocene, further emphasizing Afro-Arabia as the locus of early catarrhine evolution (Fig. 1c).

The Shumaysi Formation was deposited before the early Miocene opening of the Red Sea rift^{19–21}. It rests partly on the late Cretaceous–Eocene Usfan Formation, and is overlain in places by Miocene

sandstones of the Khulays Formation (Fig. 1b)²¹. The middle unit of the formation, from which SGS-UM 2009-002 and its associated fauna derive, represents a non-marine back-mangrove environment²⁰. Previous age estimates for the Shumaysi Formation extend from Eocene to Oligocene–early Miocene^{19,20,22}. Volcanic dykes intruding the upper Shumaysi Formation yield radioisotopic ages of 26–21 Myr (ref. 22), and the oldest lava flows overlying the formation and tuffaceous rocks interbedded in the upper unit produce dates of 25–21 Myr ago²³, indicating that the middle unit is pre-Miocene in age.

Chronostratigraphy of the middle Shumaysi Formation is refined by biochronological analysis of its mammalian assemblage. The fauna includes paenungulates and anthracotheriid artiodactyls with closely related counterparts in the upper part of the Jebel Qatrani Formation sequence of Fayum, Egypt. These taxa are less advanced than comparable animals at the late Oligocene sites of Chilga in Ethiopia and Lothidok in Kenya. They are accompanied by primitive gomphotheres and mammutids reminiscent of proboscideans found at Chilga and Lothidok but never documented in the rich fauna of the Fayum. Together, the assemblage can be temporally interpolated best between the Jebel Qatrani and Chilga Formations, making it 29–28 Myr old (Supplementary Information).

SGS-UM 2009-002 preserves most of the face, anterior neurocranium and palate, with a partial dentition of left and right I2, left C and M1–3, as well as roots of right C and P3 and left P3–4, and alveoli for left and right I1 (Fig. 2a–c). The left canine is broken apically. Some enamel has spalled off the molars, but morphometric details can be determined (Supplementary Information). There is a deep bite mark in the frontal trigon and another, possibly a fatal puncture wound, in the right side of the endocranial cavity. In addition, part of the right temporal bone is preserved, as is the right occipital condyle (Fig. 2d–g).

Salient features of SGS-UM 2009-002 include low hafting of the face on the neurocranium, snout-like projection of the midface, strong anterior convergence of temporal lines, a tubular ectotympanic (Fig. 2d, e), absence of frontal sinuses (Fig. 3a), and large, broad molars. The dental development, length of the canine roots (Fig. 3b), extent of the C–I2 diastemata, molar size, and expression of the temporal lines to form a sagittal crest indicate that the cranium is that of an adult male. Primitive catarrhine features predominate in SGS-UM 2009-002 (Supplementary Information). Together, these features comprise a distinctive taxon that differs sufficiently from early Oligocene–early middle Miocene catarrhines to be placed in a new genus and species that cannot be readily accommodated within any existing catarrhine family or superfamily (Supplementary Information).

¹Museum of Paleontology, University of Michigan, 1109 Geddes Avenue, Ann Arbor, Michigan 48109, USA. ²Department of Geological Sciences, University of Michigan, 2534 C. C. Little Building, 1100 North University Avenue, Ann Arbor, Michigan 48109, USA. ³Department of Anthropology, University of Michigan, 1085 South University Avenue, Ann Arbor, Michigan 48109, USA. ⁴Saudi Geological Survey, Paleontology Unit, PO Box 54141, Jeddah, 21514, Saudi Arabia.

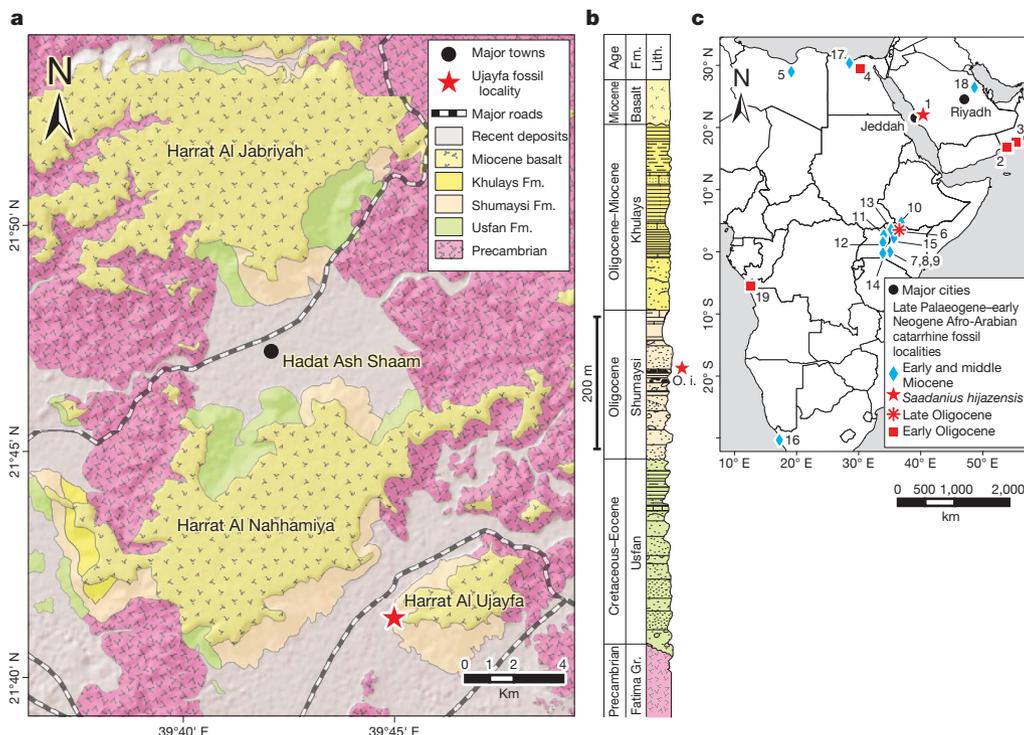


Figure 1 | Geological, geographical and stratigraphic contexts for SGS-UM 2009-002. **a**, Geological map of *Saadanius hijazensis* type site at Harrat Al Ujayfa, Saudi Arabia^{18,20}. **b**, Stratigraphic provenance of SGS-UM 2009-002. O.i., oolitic ironstone horizon. **c**, Major early Oligocene to early middle Miocene Afro-Arabian catarrhine primate sites. Key: 1, Harrat Al Ujayfa, Saudi Arabia; 2, Thaytiniti, Oman; 3, Taqah, Oman; 4, Fayum, Egypt; 5,

Gebel Zelten, Libya; 6, Lothidok, Kenya; 7, Meswa Bridge, Kenya; 8, Koru, Kenya; 9, Songhor, Kenya; 10, Buluk, Kenya; 11, Moroto, Uganda; 12, Napak, Uganda; 13, Kalodirr, Kenya; 14, Rusinga, Kenya; 15, Loperot, Kenya; 16, Ryskop, South Africa; 17, Wadi Moghara, Egypt; 18, Ad Dabtiyah, Saudi Arabia; 19, Malembe, Angola.

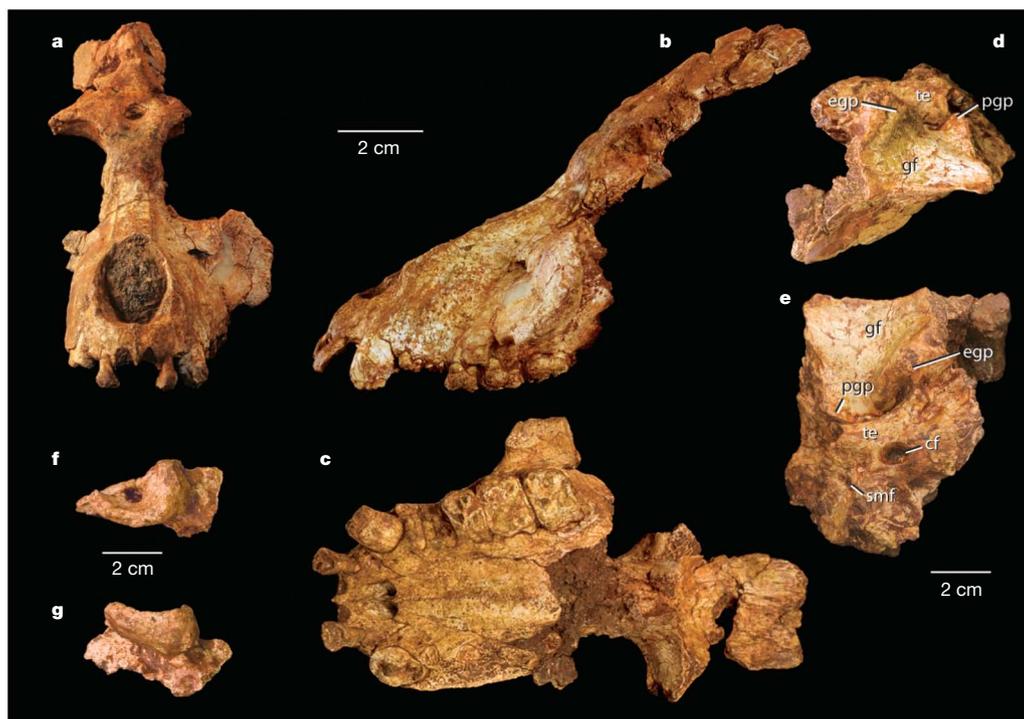


Figure 2 | Photographic images of the partial cranium SGS-UM 2009-002, type specimen of *Saadanius hijazensis* gen. et sp. nov. **a**, Cranium in anterior view. **b**, Cranium in lateral view, anterior to the left. **c**, Ventral view of cranium, anterior to the left. **d**, Anterior view of right temporal bone, ventral at top, lateral to the right. **e**, Ventral view of right temporal bone,

anterior at top, lateral to the left. **f**, Medial view of right occipital condyle, anterior to the left. **g**, Ventral view of right occipital condyle, anterior to the left. cf, carotid foramen; egp, entoglenoid process; gf, glenoid fossa; pggp, postglenoid process; smf, stylomastoid foramen; te, tubular ectotympanic.

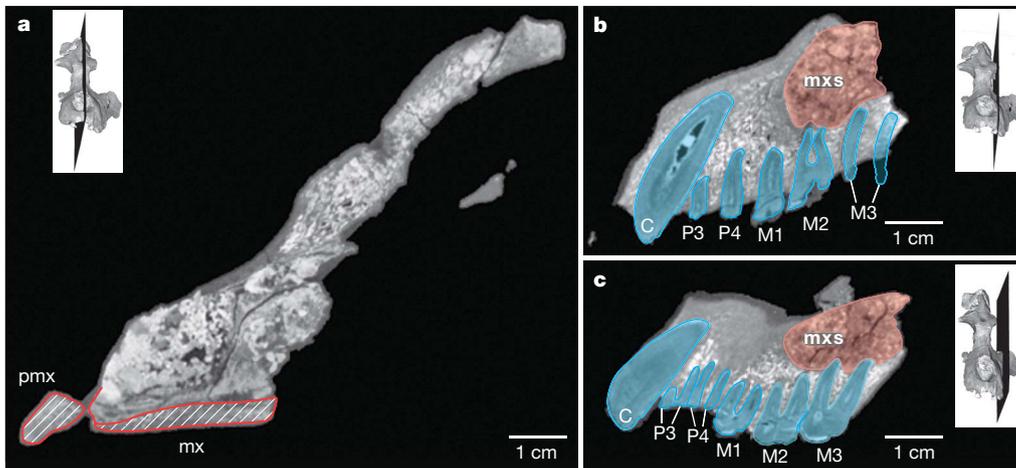


Figure 3 | Micro-CT scan images of the partial cranium SGS-UM 2009-002, type specimen of *Saadanius hijazensis* gen. et sp. nov. **a**, Midline sagittal slice. Offset of the premaxilla (pmx) and palatal process of the maxilla (mx), and thickness of the maxillary palatal process are shown by a red outline with white cross-hatching. Note the absence of frontal sinuses. **b**, Sagittal slice through the left canine. Note the large size and deeply

embedded canine root characteristic of male catarrhines. **c**, Sagittal slice through the greatest anteroposterior extension of the maxillary sinus (mxs). Note the high floor of the sinus and its anterior extension above M2. In **b** and **c** teeth and tooth roots are shaded in blue, and the maxillary sinus is shaded in red.

Order Primates, Linnaeus, 1758

Suborder Anthropoidea, Mivart, 1864

Infraorder Catarrhini, É. Geoffrey Saint-Hilaire, 1812

Superfamily Saadaniioidea nov.

Family Saadaniidae nov.

Saadanius gen. nov.

Saadanius hijazensis sp. nov.

Etymology. *Saadanius*, after *saadan* (Arabic): collective term for apes and monkeys. The specific term refers to the Al Hijaz region, western province of Saudi Arabia, where the new catarrhine was discovered. **Holotype.** SGS-UM 2009-002 (Fig. 2a–g). The type is housed in the Paleontology Unit of the Saudi Geological Survey in Jeddah, Saudi Arabia.

Locality. Southwest corner of Harrat Al Ujayfa, Al Hijaz Province, western Saudi Arabia (Fig. 1a, c).

Diagnosis. Medium-sized catarrhine (cranium similar in size to *Symphalangus*; about 15–20 kg); upper molars relatively broad, enamel thin, trigon cusps well spaced and set apart from large, distolingually situated hypocones; upper lateral incisors spatulate and probably smaller than I1s; upper canines ovoid in cross-section, with a prominent distal flange and stout, straight, elongate root (Fig. 3b); canine crown area modest relative to molar size; splanchnocranium set below the neurocranium; midfacial projection strong; orbits high; nasal bones long and narrow; nasal aperture large and oval-shaped; anterior facing and vertically oriented, low-rooted malar; strong temporal lines convergent anteriorly, enclosing a small frontal trigon; maxillary sinuses with high floor and anterior limit at M2 (Fig. 3c); no frontal sinus (Fig. 3a); palate shallow and broadest posteriorly; spacious, bifid incisive fossa; premaxillae not overlapping maxillary palatal processes (Fig. 3a); nasoalveolar clivus low; temporal bone with a short, tubular ectotympanic, broad, flat glenoid process, and massive entoglenoid process; diminutive occipital condyle. *Saadanius* is the type genus of the new family Saadaniidae, which is differentiated from other catarrhine families by features provided in the Supplementary Information.

Comparative and phylogenetic analyses of Catarrhini (Supplementary Information) indicate that *Saadanius hijazensis* is a stem catarrhine, phylogenetically close to crown catarrhines (Fig. 4) and morphologically approximate to the condition of the last common ancestor of crown catarrhines (LCA). A preponderance of features of *Saadanius* are shared with male crania of the early stem catarrhine *Aegyptopithecus zeuxis* or are intermediate between *Aegyptopithecus* and early Miocene apes (Supplementary Information).

A suite of other traits in early Miocene apes, such as frontal sinuses, increased molar trigon crowding, broadened anterior palates, more pronounced lower facial prognathism, relatively enormous male canine crowns and larger body size^{3,13,17,24–26} are absent in *Saadanius*, other stem Catarrhini and basal cercopithecoids (Supplementary Information). Distribution of these traits is consistent with the hypothesis that early Miocene apes are hominoids (Fig. 4) and that initial evolution of the group involved changes to the craniofacial region^{24,26}. The adaptive significance of these traits is probably correlated with shifts in masticatory function, diet (see, for example, ref. 15) and social behaviour, possibly related to body size increase, which itself has numerous advantages²⁷.

Early Miocene apes show few modern hominoid synapomorphies, complicating the identification of basal hominoids²⁷. The ways in which early Miocene apes differ anatomically from *Saadanius* and other stem catarrhines are crucial for providing a method for recognizing basal hominoids. For example, ‘dendropithecoids’ have resisted definitive classification because of their primitive postcranial morphology and a lack of information about cranial features such as the form of the ectotympanic^{3,18}. However, possession of frontal sinuses and relatively enormous male canines differentiate them from propliopithecoids, pliopithecoids, *Saadanius* and basal cercopithecoids, and link them with ‘proconsuloids’ as possible hominoids (see also refs 24, 26, 27). Similarly, a relatively large male canine in the late Oligocene catarrhine *Kamoyapithecus*¹⁶ may signal that it is also a basal hominoid (Supplementary Information).

Unlike propliopithecoids^{8,10} (and pliopithecoids²⁸), however, *Saadanius* shares with crown catarrhines a fully formed tubular ectotympanic, which presumably was present in the LCA and evolved only once in Catarrhini. The presence of a tubular ectotympanic in a cranium dominated by otherwise primitive catarrhine features is compelling evidence of a close phylogenetic relationship between *Saadanius* and crown catarrhines.

Neontology-based character-state analyses reconstruct the LCA cranial morphotype with a short, relatively orthognathic face, short, broad nasals and a globular braincase (see, for example, refs 12, 14). Conversely, studies incorporating observations on early Miocene apes and the basal cercopithecoid *Victoriapithecus* reconstruct an LCA morphotype with a projecting snout and tall face, long, narrow nasal bones and steep frontal with a trigon enclosed by anteriorly convergent temporal lines and supraorbital costae¹. In the second hypothesis, a stem catarrhine similar to the propliopithecoid *Aegyptopithecus* could have had a more direct role in the evolution

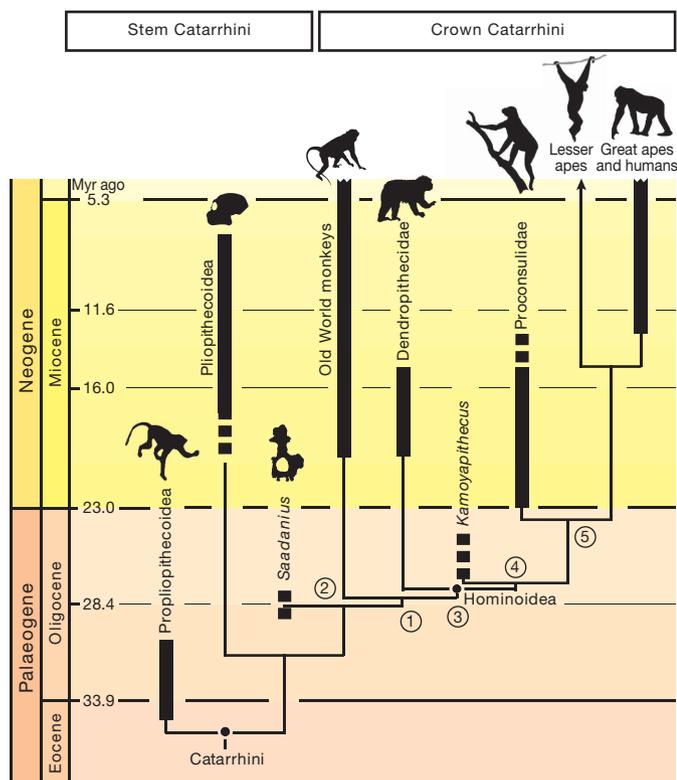


Figure 4 | Proposed relationship of *Saadanius* to other catarrhine primates.

The diagram is based on Supplementary Information and refs 1, 2, 13, 16, 17, 24, 26, 27. Thick solid vertical lines indicate known temporal ranges of taxa; thick dotted vertical lines show intervals of occurrence or possible extension for temporal ranges of taxa. The following characters define these clades: (1) *Saadanius* + crown catarrhines, presence of complete tubular ectotympanic; (2) Cercopithecoidea, bilophodont molars, absence of maxillary sinuses, absence of atriotribinal/vomeronasal functional complex, premaxillary-maxillary suture extending to top of nasals, upper canine sulcus extending onto root; (3) Hominoidea, presence of frontal sinus, male upper canines relatively very large in cross-section; (4) *Kamoyapithecus* + proconsulids + crown hominoids (including lesser apes, great apes and humans), body size increase; (5) proconsulids + crown hominoids, palate broadest anteriorly, pronounced lower facial prognathism, loss of tail, deep, narrow humeral zona conoidea, deep olecranon fossa, absence of entepicondylar foramen and epitrochlear fossa.

of later crown catarrhines, because its cranial morphology closely approximates this latter ancestral morphotype.

The second, paleontology-based, hypothesis¹ is more strongly corroborated by the presence in *Saadanius* of nearly all craniodental features predicted by it for the LCA and is further supported by the observation that many of the traits present in *Aegyptopithecus* and *Saadanius* (for example midfacial projection and long nasals^{6,8}) are retained in early Miocene apes, most notably *Afropithecus*^{15,25}, *Morotopithecus* and *Proconsul*^{17,29}. Although primitive, the consistent expression of these features suggests a conservation of the stem catarrhine male cranial morphotype well into the hominoid lineage. These features are less well developed in female propiopiithecoidea and ape crania, as a result of the strong degree of sexual dimorphism characteristic of early catarrhines (see, for example, refs 6, 10, 25). The correspondence of the intermediate temporal occurrence and intermediate morphological development of *Saadanius* between propiopiithecoidea and Miocene apes (Fig. 4 and Supplementary Information) is further suggestive of phylogenetic continuity among these taxa.

The age of the hominoid-cercopithecoidea divergence has frequently been estimated as 25–23 Myr. However, recent genomic investigation calculated an earlier incidence of this event between 34.5 and 29.2 Myr ago¹¹, nearly coincident with the entire temporal range of propiopiithecoidea⁹. It is possible that wider sampling of Afro-Arabia might

document this event within the older time interval, but no fossils of crown catarrhines have been recovered from this time span, and the oldest documented proconsulids, dendropithecoidea and cercopithecoidea only date to 23–20 Myr ago^{2–4}. *Saadanius* provides new evidence consistent with a divergence date after 29–28 Myr ago, and its comparative study offers a basis for recognition of the first hominoids subsequent to this event. If the late-Oligocene *Kamoyapithecus*¹⁶ is a hominoid, then the split occurred between 29–28 Myr and 24 Myr ago.

METHODS SUMMARY

Micro-computed tomography (micro-CT) scan imaging. SGS-UM 2009-002 was scanned with the OMNI-X Industrial Scanner at the Center for Quantitative Imaging, Pennsylvania State University. This was scanned in volume mode with a Feldkamp reconstruction algorithm.

Phylogenetic analysis. Phylogenetic analysis was carried out with TNT (Tree Analysis Using New Technology) made freely available by the Willi Hennig Society³⁰. A total of 36 characters were analysed for 19 taxa (Supplementary Information) including *Pan* and *Hylobates* as extant representatives of Hominoidea and using the basal fossil catarrhine *Aegyptopithecus* to root all trees. The Implicit Enumeration Algorithm was used to ensure that all possible trees were explored, with and without the collapse-tree option. Results in each case were identical. No characters were weighted and two characters were ordered. Consistency and Retention Indices were calculated on the basis of minimum, maximum and most-parsimonious steps for each resulting tree. Analyses were performed for all taxa and characters; all taxa, excluding postcranial characters; appropriate taxa collapsed into Dendropithecoidea and Proconsulidae and all characters; and collapsed taxa, excluding postcranial characters.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

Received 15 February; accepted 16 April 2010.

- Benefit, B. R. & McCrossin, M. L. Facial anatomy of *Victoriapithecus* and its relevance to the ancestral cranial morphology of Old World monkeys and apes. *Am. J. Phys. Anthropol.* **92**, 329–370 (1993).
- Benefit, B. R. & McCrossin, M. L. in *The Primate Fossil Record* (ed. Hartwig, W. C.) 241–253 (Cambridge Univ. Press, 2002).
- Harrison, T. in *The Primate Fossil Record* (ed. Hartwig, W. C.) 311–338 (Cambridge Univ. Press, 2002).
- Miller, E. R. *et al.* Systematics of early and middle Miocene Old World monkeys. *J. Hum. Evol.* **57**, 195–211 (2009).
- Pickford, M. Première découverte d'une faune mammalienne terrestre paléogène d'Afrique sub-saharienne. *C. R. Acad. Sci. Paris (II)* **302**, 1205–1210 (1986).
- Simons, E. L. New faces of *Aegyptopithecus* from the Oligocene of Egypt. *J. Hum. Evol.* **16**, 273–289 (1987).
- Thomas, H. *et al.* in *Fossil Vertebrates of Arabia. With Emphasis on the Late Miocene Faunas, Geology, and Palaeoenvironments of the Emirate of Abu Dhabi, United Arab Emirates* (eds Whybrow, P. J. & Hill, A.) 430–442 (Yale Univ. Press, 1999).
- Rasmussen, D. T. in *The Primate Fossil Record* (ed. Hartwig, W. C.) 203–220 (Cambridge Univ. Press, 2002).
- Seiffert, E. R. Evolution and extinction of Afro-Arabian primates near the Eocene-Oligocene boundary. *Folia Primatol. (Basel)* **78**, 314–327 (2007).
- Simons, E. L., Seiffert, E. R., Ryan, T. M. & Attia, Y. A remarkable female cranium of the early Oligocene *Aegyptopithecus zeuxis* (Catarrhini, Propiopiithecoidea). *Proc. Natl Acad. Sci. USA* **104**, 8731–8736 (2007).
- Steiper, M. E., Young, N. M. & Sukarna, T. Y. Genomic data support the hominoid slowdown and an early Oligocene estimate for the hominoid-cercopithecoidea divergence. *Proc. Natl Acad. Sci. USA* **101**, 17021–17026 (2004).
- Harrison, T. The phylogenetic relationships of the early catarrhine primates: a review of the current evidence. *J. Hum. Evol.* **16**, 41–80 (1987).
- Rae, T. C. in *Function, Phylogeny, and Fossils. Miocene Hominoid Evolution and Adaptations* (eds Begun, D. R., Ward, C. V. & Rose, M. D.) 59–77 (Plenum, 1997).
- Delson, E. & Andrews, P. in *Phylogeny of the Primates. A Multidisciplinary Approach* (eds Lockett, W. P. & Szalay, F. S.) 405–446 (Plenum, 1975).
- Leakey, M. G. *et al.* Similarities in *Aegyptopithecus* and *Afropithecus* facial morphology. *Folia Primatol. (Basel)* **56**, 65–85 (1991).
- Leakey, M. G., Ungar, P. S. & Walker, A. A new genus of large primate from the late Oligocene of Lothidok, Turkana District, Kenya. *J. Hum. Evol.* **28**, 519–531 (1995).
- Begun, D. R. in *Phylogeny of the Neogene Hominoid Primates of Eurasia* (eds de Bonis, L., Koufos, G. D. & Andrews, P.) 231–253 (Cambridge Univ. Press, 2001).
- Harrison, T. A taxonomic revision of the small catarrhine primates from the early Miocene of East Africa. *Folia Primatol. (Basel)* **50**, 59–108 (1988).
- Al-Shanti, A. M. S. Oolitic iron ore deposits in Wadi Fatima between Jeddah and Mecca, Saudi Arabia. *Saudi Arabian Dir. Gen. Min. Resources Bull.* **2**, 1–51 (1966).
- Srivastava, S. K. & Binda, P. L. Depositional history of the early Eocene Shumaysi Formation, Saudi Arabia. *Palynology* **15**, 47–61 (1991).

21. Abou Ouf, M. A. & Gheith, A. M. in *Sedimentation and Tectonics of Rift Basins: Red Sea and Gulf of Aden* (eds Purser, B. H. & Bosence, D. W. J.) 135–145 (Chapman & Hall, 1998).
22. Moltzer, J. G. & Binda, P. L. Micropaleontology and palynology of the middle and upper members of the Shumaysi Formation, Saudi Arabia. *Saudi Arabian Dir. Gen. Min. Resources Bull.* **4**, 47–76 (1981).
23. Féraud, G., Zumbo, V. & Sebai, A. $^{40}\text{Ar}/^{39}\text{Ar}$ age and duration of tholeiitic magmatism related to the early opening of the Red Sea rift. *Geophys. Res. Lett.* **18**, 195–198 (1991).
24. Rae, T. C. Mosaic evolution in the origin of the Hominoidea. *Folia Primatol. (Basel)* **70**, 125–135 (1999).
25. Leakey, R. E., Leakey, M. G. & Walker, A. C. Morphology of *Afropithecus turkanensis* from Kenya. *Am. J. Phys. Anthropol.* **76**, 289–307 (1988).
26. Rae, T. C. Miocene hominoid craniofacial morphology and the emergence of great apes. *Ann. Anat.* **186**, 417–421 (2004).
27. Kelley, J. in *Function, Phylogeny, and Fossils. Miocene Hominoid Evolution and Adaptations* (eds Begun, D.R., Ward, C.V. & Rose, M.D.) 173–208 (Plenum, 1997).
28. Begun, D. R. in *The Primate Fossil Record* (ed. Hartwig, W. C.) 221–240 (Cambridge Univ. Press, 2002).
29. Teaford, M. F., Beard, K. C., Leakey, R. E. & Walker, A. New hominoid facial skeleton from the Early Miocene of Rusinga Island, Kenya, and its bearing on the relationship between *Proconsul nyanzae* and *Proconsul africanus*. *J. Hum. Evol.* **17**, 461–477 (1988).
30. Goloboff, P., Farris, J. & Nixon, K. TNT, a free program for phylogenetic analysis. *Cladistics* **24**, 774–786 (2008).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements We thank Saudi Geological Survey (Jeddah) officials Z. A. Nawab, A. M. Al Attas and A. F. Al Khattabi for the invitation to undertake fieldwork in western Saudi Arabia; E. Mbua (National Museums of Kenya) for permission to study of catarrhine fossils in her care; A. Walker for access to micro-CT facilities at Pennsylvania State University; T. Ryan for scanning; A. Rountrey, D. Erickson and B. Miljour for assistance with interpretation of micro-CT scans, photography, and figures; T. Harrison for phylogenetic discussion and advice; E. Seiffert for CT images and photographs of propliopithecoid fossils; B. Benefit for information on the ectotympanic of *Victoriapithecus*; D. T. Rasmussen and M. Gutiérrez for information about fossil mammals from Lothidok, Kenya; M. Halawani, A. Memesh, S. Dini, C. Spencer and G. W. Hughes for information about the geology and lithostratigraphy of the research area; and E. Seiffert for improving the manuscript. The research was supported by a US National Science Foundation grant (EAR-0517773) to P.D.G.

Author Contributions I.S.Z., Y.A.A., M.A.A., A.H.N., A.M.A., S.A.A., A.O.N., A.H.M. and J.A.W. undertook the palaeontological survey, fossil collection and field geology. W.J.S. prepared the fossils. G.F.G., L.M.M. and W.J.S. performed the comparative study and phylogenetic analysis of catarrhine primates. L.M.M. and P.D.G. coordinated the micro-CT scanning. G.F.G. and W.J.S. made comparative studies of the non-primate mammalian fauna and identified the taxa. All authors contributed to the manuscript.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this article at www.nature.com/nature. Correspondence should be addressed to I.S.Z. (zalmouti@umich.edu) or W.J.S. (wsanders@umich.edu), and requests for materials to P.D.G. (gingeric@umich.edu).

METHODS

Micro-CT scan imaging. Specimen SGS-UM 2009-002 was scanned on the OMNI-X HD600 High Resolution Computed Tomography scanner in the Center for Quantitative Imaging at Pennsylvania State University. Scans were collected with the X-TEK X-ray tube with the following settings: energy settings 180 kV, 0.2 mA; source to object distance 215.03 mm; scanned with 1,440 views and five samples averaged per view; field of view 65.9 mm; $x = y = 0.0644$ mm (pixel size); $z = 0.069$ mm (slice thickness and spacing); matrix size $1,024 \times 1,024$ 16-bit TIFF images. There were 1,864 slices taken; the specimen was scanned in volume mode with a Feldkamp reconstruction algorithm.

Measurements. Standard craniodental measurements were taken of the holotype specimen of *Saadanius hijazensis* (Supplementary Table 3). All measurements were recorded to the nearest 0.01 mm using either digital callipers or a Leica S6E binocular dissecting microscope fitted with a measuring reticule.

Phylogenetic analyses. The morphological data set on which our phylogenetic analyses were based included 36 characters and 19 taxa. Besides *Saadanius*, other taxa scored included the propliopithecoid *Aegyptopithecus*, the cercopithecoid *Victoriapithecus*, Pliopithecoida (a composite taxon including *Dionysopithecus*, *Platodontopithecus*, *Pliopithecus*, *Epipliopithecus*, *Egarapithecus*, *Plesiopliopithecus*, *Anapithecus*, *Laccopithecus* and *Paidopithecus*)²⁸, the enigmatic *Kamoyapithecus*, the dendropithecids *Dendropithecus*, *Micropithecus* and *Simiolus*, the proconsulids *Afropithecus*, *Heliopithecus*, *Morotopithecus*, *Turkanapithecus*, *Nyanzapithecus*, *Rangwapithecus*, *Nacholapithecus*, *Equatorius* and *Proconsul* (combining two species *P. nyanzae* and *P. heseloni*), and the extant apes *Pan* and *Hylobates*. We also scored dendropithecids and proconsulids as single entities, which caused several polymorphic characters to be recognized. Character states were scored on original specimens housed at the Kenya National Museums, high-quality casts housed at the University of Michigan Department of Anthropology and Museum of Paleontology, or from figures and descriptions provided in the literature.

A data matrix was built with TNT (Tree Analysis Using New Technology)³⁰. Taxa and characters were defined under the Data option in TNT; character states

were then assigned to each taxon on the basis of our scoring. Using the Character Settings option in TNT we were able to define characters as additive (ordered) or non-additive (unordered) and to include or exclude characters to explore different analysis options. Our matrix was then saved as a *.tnt file using the Save Data option.

This data matrix was then analysed with the Implicit Enumeration Algorithm under the Analyse menu in TNT to ensure that all possible trees were explored, both with and without the collapse-tree option (results in each case were identical). Phylogenetic analysis was performed using the basal fossil catarrhine (propliopithecoid) *Aegyptopithecus* to root all trees. All characters were treated as being of equal weight, and two characters were ordered (16, upper canine size and 30, presence or absence of an entepicondylar foramen on the distal humerus; see Supplementary Table 5).

Consistency Index (CI) and Retention Index (RI) were calculated on the basis of minimum (MIN) and maximum (MAX) and most-parsimonious (MP) steps for each resulting tree (using the show max-min option in TNT). $CI = MIN/MP$; $RI = (MAX - MP)/(MAX - MIN)$.

Analyses were performed in four ways: for all taxa using all characters (Supplementary Fig. 3c); for all taxa, excluding postcranial characters (Supplementary Fig. 3d); for appropriate taxa collapsed into Dendropithecidae and Proconsulidae using all characters (Supplementary Fig. 3a); and for collapsed taxa, excluding postcranial characters (Supplementary Fig. 3b). Trees were examined with the View Trees option in TNT, and consensus trees were viewed with the TNT Consensus option in the Trees menu. The TNT Optimize menu was used to view tree statistics (lengths, branch lengths and min-max) and to explore the distribution of different character states by mapping characters and synapomorphies onto trees.

As a final test of the trees produced by TNT, we saved our *.tnt file as a NEXUS file and analysed that matrix using PAUP with the Branch-and-Bound option to ensure finding the shortest trees. Results were identical to those produced in TNT.